

Ichnusomunda sacchii, a New Hygromiid Snail from Sardinia Island (Western Mediterranean): An Intriguing Case of Homoplasy in the Anatomical Organization (Pulmonata: Hygromiidae)

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Abstract. *Ichnusomunda sacchii*, new genus and new species, is described from Sardinia. The new genus is anatomically characterized by: right ommatophore retractor independent of genitalia; penial nerve from right pedal ganglion; left lateral lobe of pallial margin long; vagina with digitiform glands and 0 + 2 dart-sac complex, the latter consisting of elongated, wide, cylindrical basal portion, joined perpendicular to distal vagina, at the apex of which two stylophores open side-by-side; outer stylophore small, globular, with thick, muscular walls, secreting dart; inner stylophore long and slender, with thin walls and wide, empty (dartless) lumen, bent to adhere to upper side of basal portion; penis with long, cylindrical penial papilla having three basal frenula. This combination of anatomical characters is unique and distinct from those in the other genera of the Hygromiidae. Some of these characters (pedal penial innervation; three frenula at the base of penial papilla) are shared with *Cernuella* (*Cernuella*) and *Cernuella* (*Xeroamanda*), others (basal portion of dart-sac complex; structure of inner stylophore) with *Xeromunda*, *Xerolenta*, and *Pseudoxerophila*.

I. sacchii has a limited distribution, being known only from the type locality, the sand dunes of Riu Piscinas, a very important biotope of western Sardinia (no. 20/35 in the checklist of the Società Botanica Italiana; no. ITB000031 of the "Nature-2000 Web"). Although *I. sacchii* is very common in this site, its limited distribution is a clear risk factor in the face of man-made modifications to the peculiar habitat in which it lives.

INTRODUCTION

Sardinia and Corsica have a rich hygromiid fauna characterized by a number of endemic taxa, e.g., *Cyrtosuccinea corsica* (Shuttleworth, 1844), *Ichnusotricha bernini* Giusti & Manganelli, 1987, *Nienhuisiella antonellae* Giusti & Manganelli, 1987, *Xerosecta dohrni* (Paulucci, 1882), *X. hillyeriana* (Paulucci, 1882), and others with a reduced disjunct distribution, e.g., the Tyrrhenian *Tyrrheniellina josephi* (Giusti & Manganelli, 1990), and the West Mediterranean *Ganula lanuginosa* (Boissy, 1835) and *Pollo-neriella contermina* (Pfeiffer, 1847) (Carrada et al. 1967; Giusti & Castagnolo, 1983; Giusti & Manganelli, 1987, 1989; Manganelli et al., 1995).

The recent study of material collected in dune habitats by Prof. C. Sacchi of the Dipartimento di Biologia of the University of Pavia (Italy) has led to the identification of another, previously unknown xerophilous hygromiid, very peculiar in the structure of the distal genitalia.

MATERIALS AND METHODS

Whole shells were photographed under the light microscope (Wild M5A). All dimensions (shell height, maximum shell diameter, aperture height, and aperture diameter) were measured using calipers.

Living specimens were drowned in water, then fixed and preserved in 75% ethanol, buffered with NaHCO₃. The bod-

ies were isolated after crushing the shells, and dissected under the light microscope (Wild M5A) using very thin pointed watchmaker's tweezers. Anatomical details were drawn using a Wild camera lucida. Anatomical parts were measured using a millimetric lens on the same microscope.

Radulae were manually extracted from the buccal bulbs, washed in pure 75% ethanol, mounted on copper blocks with conductive glue, sputter-coated with gold, and studied using a Philips 505 SEM.

The material examined is listed as follows: locality, municipality, and province names in parenthesis, UTM reference, collector(s), date, number of specimens in parenthesis. Locality names were according to the official 1:25,000 scale map of Italy (series M 891, sheet 225 IV SO) and UTM references were according to the official 1:100,000 scale map of Italy (series M 691, sheet 224–225).

Unless otherwise indicated, all the specimens illustrated are kept in the Giusti Collection (Dipartimento di Biologia Evolutiva, Via Mattioli 4, I-53100 Siena, Italy).

SYSTEMATICS

Ichnusomunda Giusti & Manganelli, gen. nov.

Type species: *Ichnusomunda sacchii* sp. nov.

Diagnosis: Pulmonate, hygromiid snail with shell dextral, small, globose, and anatomically characterized by: (1) right ommatophore retractor independent of genitalia; (2)

penial nerve from right pedal ganglion; (3) left lateral lobe of pallial margin long; (4) vagina with digitiform glands and 0 + 2 dart-sac complex, the latter consisting of elongated, wide, cylindrical basal portion, perpendicularly joined to distal vagina, at whose apex two stylophores open side-by-side; outer stylophore small, globular, with thick, muscular walls, secreting dart; inner stylophore long and slender, with thin walls and wide, empty (dartless) lumen, bent to adhere to upper side of basal portion; (5) penial complex consisting of flagellum, epiphallus and penis; penis with long, cylindrical penial papilla having three basal frenula.

Origin of the name: *Ichnusomunda*, gender feminine, is derived from "Ichnusa," the Latin name of Sardinia (in Pliny), and the suffix "munda" from *Xeromunda*, the Mediterranean, hygromiid genus superficially (conchologically), most similar to the new genus.

Ichnusomunda sacchii Guisti & Manganelli, sp. nov.

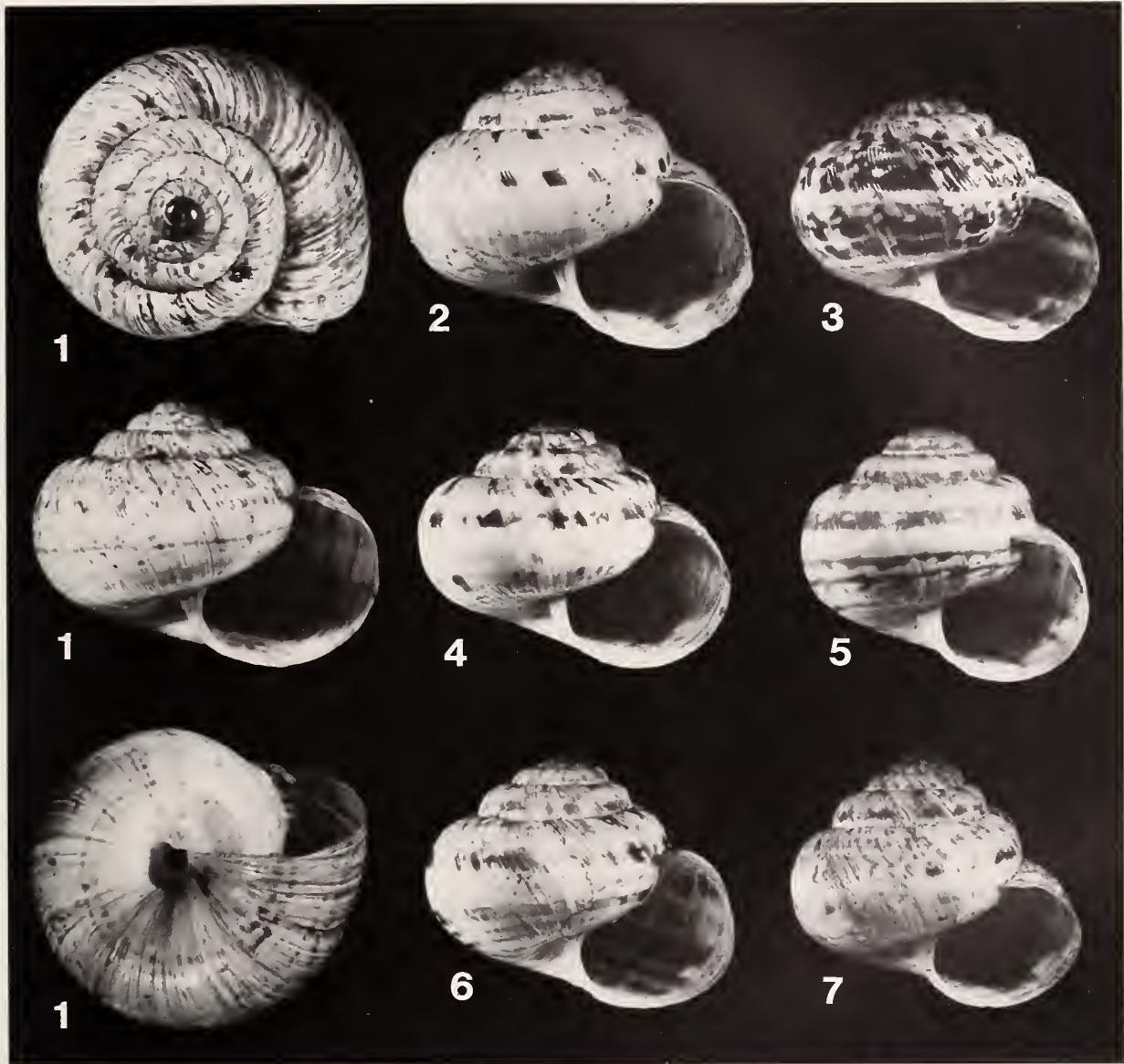
Diagnosis: *Ichnusomunda sacchii* is the only known species of the genus *Ichnusomunda*. Consequently its diagnosis is the same as that of the genus.

Shell (Figures 1–7): dextral, globose, small, hairless, whitish, with two to eight ginger brown bands usually fragmented into rows of spots of variable size, with very fine, regularly spaced riblets clearly visible from sutures to periphery of whorls, and fading out from periphery of last whorl to umbilicus (this portion consequently has a smooth appearance). Spire conical, consisting of $5\frac{1}{8}$ – $5\frac{1}{2}$ (in fully adult specimens; protoconch consisting of ca. $1\frac{3}{4}$ whorls) convex, regularly increasing whorls separated by deep sutures; last whorl slightly dilated and sometimes descending slightly near aperture. Umbilicus open, very small, partly covered by reflected columellar margin of peristome. Aperture oblique, usually rounded, rarely slightly elliptical or squared, with very thin to absent internal rib. Peristome not thickened, slightly reflected at lower and columellar margin (with upper vertex starting at, or just above, periphery of last whorl). Dimensions (N = 50). Shell diameter: 8.8 ± 0.8 mm (range: 7.8–10.3 mm); shell height: 7.3 ± 0.7 mm (range: 6.5–8.8 mm); aperture diameter: 5.2 ± 0.5 mm (range: 4.6–6.0 mm); aperture height: 4.3 ± 0.4 mm (range: 3.9–5.3 mm).

Body (Figures 8–9): Soft parts yellowish to pale pinkish. Mantle border with five lobes: right and left dorsal bordering upper margin of pneumostome, not particularly long; left lateral long, in form of thin lamina with upper vertex ending quite close to apex of left dorsal; subpneumostomal, variable in shape, usually triangular; right lateral, elongated triangular with base situated just below anal opening. Mantle border rather angled at right upper vertex; foot with non-partite sole of holopode type; walls of pallial cavity colorless, or with small black stripes or

spots (larger spot close to mantle border near pneumostome and anus; transverse stripes border minor, transverse vessels; one longitudinal line along pulmonary vein).

Genitalia (Figures 10–22): Eight specimens dissected (five of which measured): General scheme of the semi-diaulic monotrematic type. Large hermaphrodite gonad (ovotestis) consisting of acini, ducts of which converge into first hermaphrodite duct having initial portion very slender, then widening to function as seminal vesicle. First hermaphrodite duct ending in clublike "talon" adhering to internal side of large, beanlike albumen gland. Talon consisting of two distinct structures, one long, slender (digitlike), outward-projected, containing seminal receptacles (treelike system of tubules, ending in three to four branches), other, functioning as fertilization chamber, globose (saclike), with thin walls and wide lumen. Second hermaphrodite duct (ovispermiduct) arising from base of albumen gland, and consisting of female channel (uterine portion of ovispermiduct containing seminal groove) and prostate gland (with sperm groove) fused to define single lumen. Short (1.6–2.6 mm) free oviduct following female channel. Duct of bursa copulatrix arising from where proximal vagina follows free oviduct, long (6.8–8.1 mm), initially not or very slightly flared, ending in large, ovoidal to saclike bursa copulatrix (gametolytic gland). Long slender, externally smooth, apically pointed, oval in transverse section spermatophore sometimes present inside duct of bursa copulatrix and bursa copulatrix. Proximal vagina in two parts: one (from where duct of bursa copulatrix begins to base of digitiform glands) very short (0.6–0.7 mm), other (from base of digitiform glands to where basal portion of dart-sac complex enters vagina) longer (1.6–3.0 mm). Three to four tufts of branched, long, slender digitiform glands arising from vagina, one to two tufts opposite other two. Elongated dart-sac complex (DSC) entering distal vagina at right angle, and having two stylophores, on same side of vagina (0 + 2 DSC); dart-sac complex consisting of wide, cylindrical basal portion (2.6–3.2 mm) at apex of which two stylophores opening side-by-side; on internal upper wall of basal portion two large pleats originating in proximal vagina distally fusing to form calotte covering outer stylophore opening (and dart tip when dart present); kind of pleat of pale yellowish glandular tissue bordering distal portion of pleats and calotte, also visible from outside; outer stylophore small (length about 0.6–0.7 mm), globular, with thick, muscular walls and small, short lumen in which dart secreted; dart very short (0.6–0.7 mm), oval in transverse section near base, spear-shaped (with one lateral wing on opposite sides) and lenslike in transverse section at tip; inner stylophore ("nebensack" or accessory sac), difficult to discern externally because bent toward vagina and fastened to upper side of basal portion by strips of tissue; when strips removed, inner stylophore revealing long (2.0–2.4 mm), clublike, sometimes slightly twisted

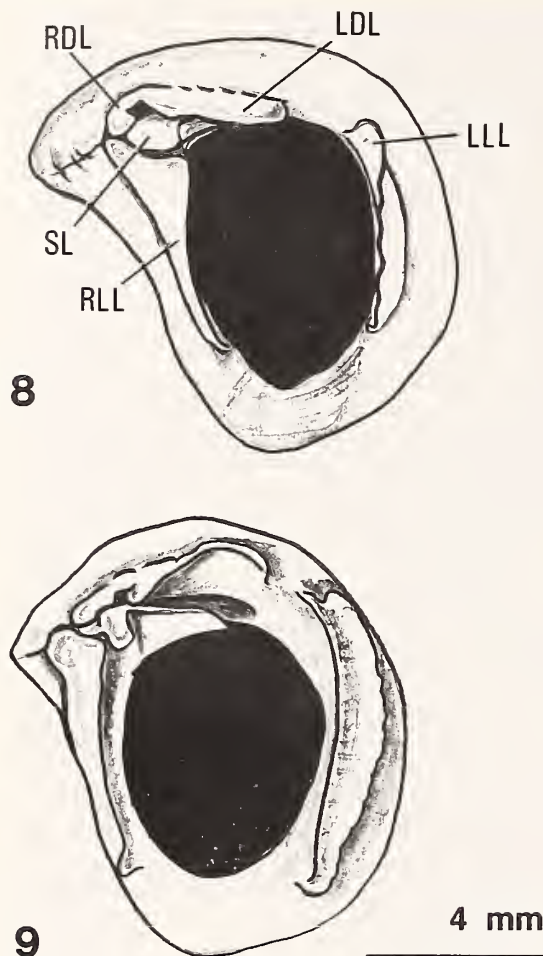


Explanation of Figures 1 to 7

Shells of *Ichnusomunda sacchii* Giusti & Manganelli, gen. & sp. nov., from Is Arenas, Cuccuru Pranu (Arbus, Cagliari, Sardinia, Italy), 32SMJ5378, G. Manganelli, L. Manganelli & G. Cappelli leg. 19 October 1995. Holotype (1) in the Museo di Zoologia dell'Università di Firenze (Firenze, Italy), MZUF 11566. Other specimens in Giusti Collection (Dipartimento di Biologia Evolutiva, Via Mattioli 4, I-53100 Siena, Italy). All $\times 3.5$.

with thin walls and rather wide empty cavity. Penial complex consisting of flagellum, epiphallus, and penis; flagellum very short (0.7–0.9 mm), ending level with where vas deferens enters penial complex and epiphallus begins; epiphallus long (6.0–8.2 mm), ending where penial retractor muscle contacts penial complex wall and penis begins; penis (from where penial retractor muscle inserts to distal vagina close to base of genital atrium) about half epiphallus length (3.0–3.7 mm), entering distal vagina,

slightly closer to genital atrium than base of dart-sac complex; penis consisting of very short proximal portion (from where penial retractor muscle ends to base of penial papilla; length: 0.6–0.9 mm) and longer distal portion (in which penial papilla lodged; length: 2.4–2.8 mm); penial papilla rather long (2.0–2.5 mm), conical, with three basal frenula connecting it to inner surface of penis wall, having apical opening, transverse section of which revealing compact structure (only one, small lacuna half-



Explanation of Figures 8 and 9

Mantle border of two specimens of *Ichnusomunda sacchii* Giusti & Manganelli, gen. & sp. nov., from Is Arenas, Cuccuru Pranu (Arbus, Cagliari, Sardinia, Italy), 32SMJ5378, G. Manganelli, L. Manganelli & G. Cappelli leg. 19 October 1995. Giusti Collection (Dipartimento di Biologia Evolutiva, Via Mattioli 4, I-53100 Siena, Italy). Key: LDL, left dorsal lobe; LLL, left lateral lobe; RDL, right dorsal lobe; RLL, right lateral lobe; SL, subpneumostomal lobe.

way between outer wall and lumen); fascia containing pale yellowish glandular tissue (difficult to discern from outside), bordering opening of penis into distal vagina, and forming sphincterlike ring; genital atrium very short (1.0–1.6 mm), opening on right side of body near base of right ommatophore; large, raised, crestlike, pleat (possibly “organ of contact” similar to that in other hygromiids and helicids) on internal wall of genital atrium on same side as penis enters genital atrium.

Radula: Consisting of many rows each of about 45–47 teeth; central tooth with large tricuspid crown, mesocone more than twice ectocone height; first lateral teeth with

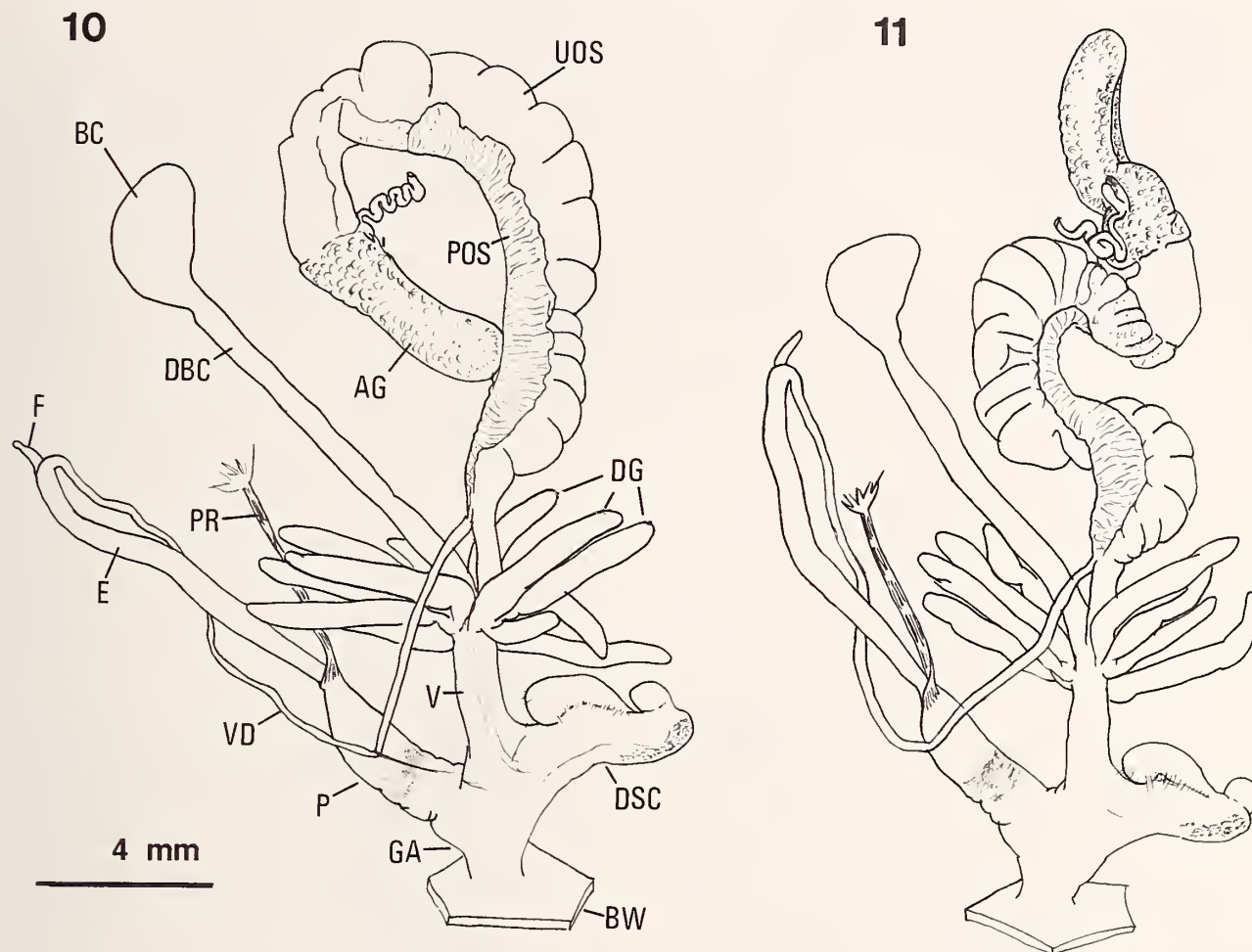
bicuspid crown, mesocone long and robust, inner side of mesocone somewhat milled, ectocone small (ca. one-half mesocone height) and sharply pointed; last lateral teeth with bicuspid crown, mesocone long with very small indentation on inner side at about two-thirds of mesocone height, ectocone small, slender, and sharply pointed; latero-marginal teeth with bicuspid crown, mesocone more slender than in lateral teeth, with small protuberance on inner side at about two-thirds of mesocone height, ectocone small, slender and sharply pointed; extreme marginal teeth with crown composed of mesocone, usually with one to two small protuberances on inner side and still evident ectocone, frequently split into two to three small, sharp points.

Type locality: Sardinia Island, Is Arenas, Cuccuru Pranu (municipality of Arbus, province of Cagliari), 32TMJ5378.

Type material: Holotype from Is Arenas, Cuccuru Pranu (Arbus, Cagliari), 32SMJ5378, G. Manganelli, L. Manganelli & G. Cappelli leg. 19 October 1995 in the Museo di Zoologia dell'Università di Firenze (Florence, Italy), MZUF 11566 and 388 paratypes from the following localities: Is Arenas, near the mouth of Riu di Naracauli (Arbus, Cagliari), 32TMJ5376, G. Manganelli & F. Giusti leg. 17 May 1994 (130 shells); 5 in the Museo di Zoologia dell'Università di Firenze (Florence, Italy), MZUF 11567; 5 in Museo Regionale di Scienze Naturali (Turin, Italy), MRSN 121.1-5. Is Arenas, Sisca (Arbus, Cagliari), 32SMJ5377, G. Manganelli, L. Manganelli & G. Cappelli leg. 18 October 1995 (46 shells and 9 living specimens; 5 shells in the Museo di Zoologia dell'Università di Firenze, MZUF 11568; 5 shells in Museo Regionale di Scienze Naturali, Torino, MRSN 122.1-5). Is Arenas, Cuccuru Pranu (Arbus, Cagliari), 32SMJ5378, G. Manganelli, L. Manganelli & G. Cappelli leg. 19 October 1995 (41 shells and 50 living specimens; 5 shells in Museo Regionale di Scienze Naturali, Torino, MRSN 120.1-5). Is Arenas, Riu Piscinas (Arbus, Cagliari), 32SMJ57 C. Sacchi leg. 18 March 1982 (90 shells and 22 juvenile living specimens).

Origin of the name: The new species is named after Prof. Cesare Sacchi (Pavia, Italy), in appreciation of his friendship and esteem for his many important contributions to the ecology and biogeography of non-marine mollusks of the western Mediterranean.

Taxonomy: Before introducing a new species we checked that a name was already available for the new species among the new names created by past authors for Sardinian hygromiids. Five xerophilous hygromiids (see Table 1; Figures 23–27) have been described from Sardinia. Two of these, *Helix dohrni* Paulucci, 1882, and *Helix hillyeriana* Paulucci, 1882, are *Xerosecta* species (Manganelli et al., 1995). The others are in need of re-



Explanation of Figures 10 and 11

Genitalia (gonad excluded) of two specimens of *Ichnusomunda sacchii* Giusti & Manganelli, gen. & sp. nov., from Is Arenas, Cuccuru Pranu (Arbus, Cagliari, Sardinia, Italy), 32SMJ5378, G. Manganelli, L. Manganelli & G. Cappelli leg. 19 October 1995. Giusti Collection (Dipartimento di Biologia Evolutiva, Via Mattioli 4, I-53100 Siena, Italy). Key: AG, albumen gland; BC, bursa copulatrix; BW, body wall; DBC, duct of bursa copulatrix; DG, digitiform glands; DSC, dart-sac complex; E, epiphallus; F, flagellum; GA, genital atrium; P, penis; POS, prostatic portion of ovispermiduct; PR, penial retractor muscle; UOS, uterine portion of ovispermiduct; V, vagina; VD, vas deferens.

vision, but are not related to the new species because they are based on specimens of *C. (Cernuella)*.

Among these species, that having a shell most similar to *I. sacchii* is *H. dohrni*, but anatomical examination of specimens from many localities of northern Sardinia (including the neighborhood of Sassari) proved that this species belongs to the genus *Xerosecta*.

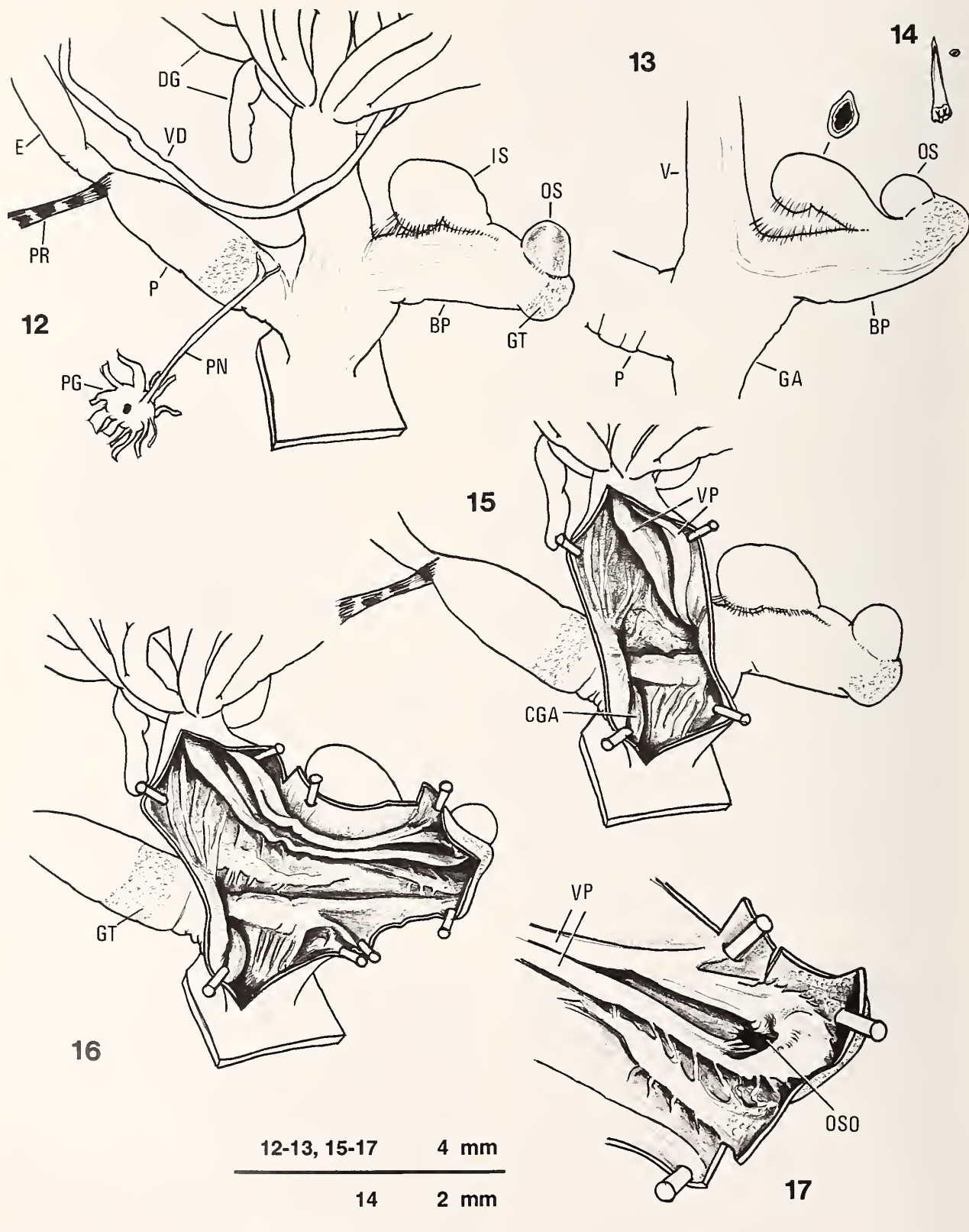
Habitat: Sandy dunes. At base of bushes or under sparse vegetation or litter, usually hidden in the sand (during the day and in the dry season).

Status and conservation: *Ichnusomunda sacchii* is known only from the sandy dunes of Is Arenas. Despite intensive research along the Sardinian coasts, no other

population of this species has been found. In fact, in similar habitats *I. sacchii* is replaced by the widely distributed *Polloneriella contermina* (Pfeiffer, 1848) and sometimes by *Xerosecta dohrni* (Paulucci, 1882) to the north.

The most extensive sand dunes of the northwestern Mediterranean are found in Sardinia, but since the end of the fifties, some of these peculiar biotopes (Is Arenas, Buggerru, Marina di Gonnessa) have been altered by reforestation with pines (especially *Pinus halepensis*) in order to arrest the advance of the dunes onto farmland. Building speculators have caused further damage, currently limited to a few areas of the south coast (De Marco & Mossa, 1983).

The biotope of Riu Piscinas (no. 20/35 in the checklist



of the Società Botanica Italiana; no. ITB000031 of the "Nature-2000 Web") is one of the most important and least altered. The dunes stretch about a kilometer inland, achieving an altitude of about 100 m on the left bank of Riu Naracauli, where the quantity of sand is greatest. The biotope of Riu Piscinas has plant communities typical of the dunes of Sardinia, e.g., *Ammophiletum arundinaceae*, *Crucianelletum maritima*, *Centaureo-Ononidetum ramosissimae*, and *Pistacio-Juniperetum macrocarpae*.

With regard to the fauna, the coleopteran biocenosis, characterized by localized Sardinian endemics, such as *Typhoeus hiostius* Gené, 1836 (Coleoptera, Geotrupidae), *Calicnemis sardiniensis* Leo, 1895 (Coleoptera, Dinastidae), and *Thorectes sardous* Erichson, 1847 (Coleoptera, Geotrupidae) (Cassola, 1978; A. Casale, personal communication) is of considerable interest. *I. sacchii* is undoubtedly the most interesting and important animal species living in the biotope. Although *I. sacchii* is very common in this site, its limited distribution would be a clear risk factor in the face of man-made modifications to the peculiar biotope in which it lives. Hence, it can be defined as vulnerable (VU: D2; see IUCN, 1994).

DISCUSSION

The new species shows a unique combination of anatomical characters that prevents its inclusion in any other known genus of the Hygromiidae. Consequently, a new genus is necessary to accommodate it. The new genus, *Ichnusomunda*, is easily distinguishable from all the other hygromiid genera (Tables 2, 3).

The right ommatophore free of the genitalia and the dart-sac complex (consisting of an inner dartless stylophore and an outer dart-secreting stylophore) limits the comparison to the hygromiid genera traditionally assigned to the "Helicellinae." They include some genera with 0 + 2 DSC, e.g., *Candidula* Kobelt, 1871, *Cernuella* Schlüter, 1838 (with three subgenera: *C. (Cernuella)*, *Xeromanda* Monterosato, 1892, and *Xerocincta* Monterosato, 1892), *Cernuellopsis* Manganelli & Giusti, 1988, *Microxeromagna* Ortiz de Zarate Lopez, 1950, *Polloneriella* Alzona & Alzona Bisacchi, 1940, *Xeromunda* Monterosato, 1892, *Xeroplana* Monterosato, 1892, and *Xerosecta* Monterosato, 1892), and others with 2 + 2 DSC,

e.g., *Helicella* Férussac, 1821, *Helicopsis* Fitzinger, 1833, *Helicotricha* Giusti et al., 1992, *Pseudoxerophila* Westerland, 1879, *Xerolenta* Monterosato, 1892, *Xeropicta* Monterosato, 1892, *Xerotricha* Monterosato, 1892. Some of the genera with 0 + 2 DSC are thought to form monophyletic groups with others with 2 + 2 DSC: *Candidula* with *Helicella* (Hausdorf, 1988; Giusti et al., 1992), *Xeromunda* with *Pseudoxerophila* and *Xerolenta* (Hausdorf, 1988; Giusti et al., 1992), *Microxeromagna* and *Xerosecta* with *Helicotricha* (Giusti et al., 1992).

Ichnusomunda shares the pedal innervation of the penis with *Candidula* (and its sister group, the 2 + 2 DSC *Helicella*), *Cernuella*, *Cernuellopsis*, and *Xeroplana*. It also shares three frenula connecting the penial papilla to the penis walls with two of the three subgenera of *Cernuella*, *C. (Cernuella)* and *C. (Xeroamanda)*. *Ichnusomunda* differs markedly from all of those by virtue of a completely different organization of the dart-sac complex.

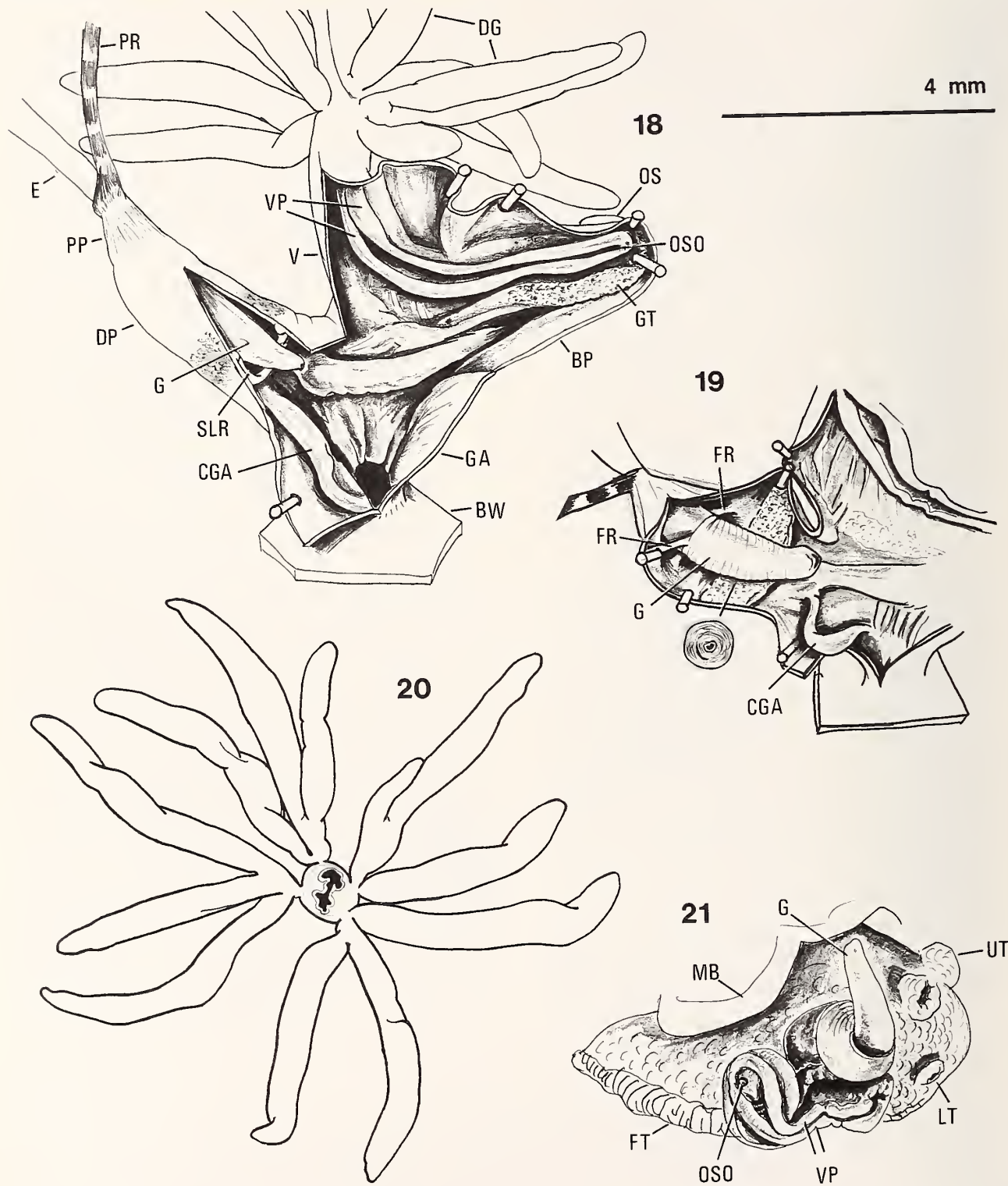
Candidula (and the 2 + 2 DSC *Helicella*) has a short left lateral lobe of the pallial margin and a dart-sac complex which lies side-by-side with the vagina so that its longitudinal axis is parallel or forms a very acute angle with that of the vagina. The DSC lacks a basal portion and consists of a large bottle-shaped outer stylophore and a vestigial inner stylophore. The latter is not visible from the outside and is hardly recognizable as such even when the dart-sac complex is dissected. The stylophores open into a large tonguelike structure (for *Candidula* see Hausdorf, 1988: 15–17, figs. 10, 11 [*C. unifasciata* (Poirét, 1801) and *C. gigaxii* (Pfeiffer, 1850)]; for *Helicella* see Giusti & Manganelli, 1989: figs. 6, 7, 9C [*H. itala* (Linnaeus, 1758)]).

Cernuella differs in having a dart-sac complex which lies side-by-side with the proximal vagina so that the wall of the inner stylophore adheres to that of the vagina (the longitudinal axis of the dart-sac complex forms an acute angle with that of the vagina). The DSC lacks a basal portion and has clearly visible outer and inner stylophores of quite similar shape and size. The openings of the two stylophores are distant from each other and situated inside the groove of the dart-gun (a conical structure through which the dart is expelled) (for *Cernuella (Cernuella)* see Hausdorf, 1988: 18, fig. 12 [*C. virgata* (Da Costa, 1778)]).

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Explanation of Figures 12 to 17

Details of distal genitalia of specimens of *Ichnusomunda sacchii* Giusti & Manganelli, gen. & sp. nov., from Is Arenas, Cuccuru Pranu (Arbus, Cagliari, Sardinia, Italy), 32SMJ5378, G. Manganelli, L. Manganelli & G. Cappelli leg. 19 October 1995. The distal genitalia *in toto*, with penial nerve originating from pedal ganglion (12); detail of dart-sac complex with transverse section of inner stylophore (13); the dart (14); dissection of vagina and basal portion of dart-sac complex (15–17). Giusti Collection (Dipartimento di Biologia Evolutiva, Via Mattioli 4, I-53100 Siena, Italy). Key: BP, basal portion of dart-sac complex; CGA, crestlike structure of genital atrium; DG, digitiform glands; E, epiphallus; GA, genital atrium; GT, glandular tissue; IS, inner stylophore; OS, outer stylophore; OSO, outer stylophore opening; P, penis; PG, pedal ganglion; PN, penial nerve; PR, penial retractor muscle; V, vagina; VD, vas deferens; VP, vaginal pleats.



Manganelli & Giusti, 1988: 345–346, figs. 4A–G, 5A–F, 14A, B [*C. virgata* and *C. cisalpina* (Rossmässler, 1837)]; for *Cernuella* (*Xeroamanda*) see Manganelli & Giusti, 1988: fig. 6A–E [*C. caruanae* Kobelt (1888)]; Manganelli et al. 1996: figs. 5–9 [*C. amanda* Rossmässler, (1838)]; for *Cernuella* (*Xerocincta*) see Manganelli & Giusti, 1988:348, 350, figs. 7A–H, 14C [*C. neglecta* (Draparnaud, 1885)].

Cernuellopsis differs in having a short left lateral lobe of the pallial margin and a dart-sac complex that lacks a basal portion and is also asymmetrically disposed with respect to the vagina. The proximal vagina terminates, forming an acute angle with the DSC, on the side of the inner stylophore facing the outer stylophore (not between the two stylophores: it is not possible to section the dart-sac complex and vagina into two specular halves). *Cernuellopsis* also differs from *Ichnusomunda* in the internal structure of the dart-sac complex and vagina. It has a cylindrical “dart-gun,” with an open base (that facing the proximal vagina) and an apex (that facing genital atrium) that extends into a short, conical tube. It has a pleat that extends from the inner walls of the proximal vagina to the dart-sac area, where it branches, giving rise to a pleat that penetrates the lumen of the “dart-gun” on one side and to a tongue-like structure that widens to laterally embrace the “dart-gun” cylindrical structure on the other side. The openings of the two stylophores (visible only after dissection of the cylindrical structure) are distinct and not far from each other (that of the outer stylophore is closer to the apex of the dart-gun) (for the only known species of *Cernuellopsis*, *C. ghisottii* see Manganelli & Giusti, 1988:334–336, 338, figs. 1A–G, 2A–E, 14L).

Xeroplana differs in having a dart-sac complex that lies side-by-side with the proximal vagina so that the wall of the inner stylophore adheres to that of the vagina (the longitudinal axis of the dart-sac complex forms an acute angle with that of the vagina). The DSC lacks a basal portion and has well-formed outer and inner stylophores of quite similar shape and size. The dart-sac complex contains a small “dart-gun” that projects into the distal vagina; the dart-gun is similar in shape, but smaller than that of *Cernuella* and is open to the tip. The openings of the two stylophores are independent, one (that of the in-

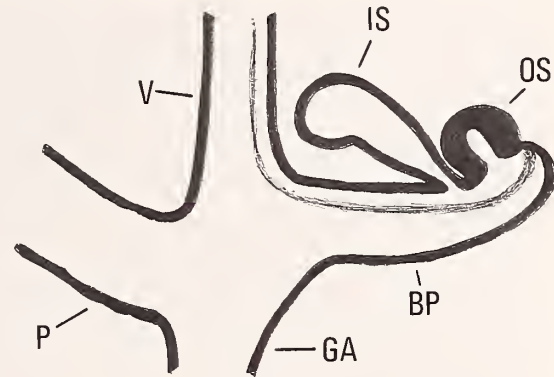


Figure 22

Scheme of dart-sac complex of *Ichnusomunda sacchii* Giusti & Manganelli, gen. & sp. nov. Key: BP, basal portion of dart-sac complex; GA, genital atrium; IS, inner stylophore; OS, outer stylophore; P, penis; V, vagina.

ner stylophore) before the other, both inside the groove of the dart-gun. The dart is peculiar with respect to those of the other genera: it has only one lateral wing that arises at one-third of its length and ends at the tip (in transverse section near tip it is polygonal, with a lateral, hooklike projection) (for *Xeroplana* see Manganelli & Giusti, 1988: figs. 12A–E, 14D [*X. doumeti* (Bourguignat, 1876), as *X. lacosteana* (Morlet, 1881)]; Manganelli et al., 1997: figs. 4–12 [*X. idia* (Issel, 1885)]).

Unlike the genera discussed above, which share pedal innervation of the penis with *Ichnusomunda*, certain other genera, e.g., *Xeromunda* and the 2 + 2 DSC *Xerolenta* and *Pseudoxerophila*, share a basal portion connecting the stylophores to the vagina with *Ichnusomunda*. It also shares a similar inner stylophore structure with *Pseudoxerophila* and one species of *Xeromunda* (*X. peloponnesia* Hausdorf, 1990).

Xeromunda, *Xerolenta*, and *Pseudoxerophila* differ from *Ichnusomunda* by virtue of cerebral innervation of the penis and other characters. In particular, *Xeromunda* differs from *Ichnusomunda* in that it has a short left lateral lobe of the pallial margin, a long proximal penis (about half of whole penis length), no frenula connecting

←

Explanation of Figures 18 to 21

Details of distal genitalia of specimens of *Ichnusomunda sacchii* Giusti & Manganelli, gen. & sp. nov., from Is Arenas, Cuccuru Pranu (Arbus, Cagliari, Sardinia, Italy), 32SMJ5378, G. Manganelli, L. Manganelli & G. Cappelli leg. 19 October 1995. Dissection of penis to show penial papilla (18, 19); the digitiform glands (20); during copula distal parts (penis, basal portion of dart-sac complex and genital atrium) are extroflexed from genital opening (21). Giusti Collection (Dipartimento di Biologia Evolutiva, Via Mattioli 4, I-53100 Siena, Italy). Key: BP, basal portion of dart-sac complex; BW, body wall; CGA, crestlike structure of genital atrium; DG, digitiform glands; DP, distal penis; E, epiphallus; FR, frenulum; FT, foot; G, penial papilla; GA, genital atrium; GT, glandular tissue; LT, lower tentacle; MB, mantle border; OS, outer stylophore; OSO, outer stylophore opening; PP, proximal penis; PR, penial retractor muscle; SLR, sphincterlike ring; UT, upper tentacle; V, vagina; VP, vaginal pleats.

Table 1

Nominal taxa of the species group introduced for Sardinian xerophilous hygromiids.

X[erophila]. balteata Pollonera, 1892:4–5.

Type material: 3 syntypes (MRSNT 149), one of which selected as lectotype (Figure 23).

Type locality: "Tudu Mannu presso Cagliari [Tudu Mannu near Cagliari] (Camerano)."

Status: a nominal species of *C. (Cernuella)* in need of revision.

Helix Dohmi Paulucci, 1882:252–253, 1883: pl. 7, figs. 3, 3a, b.

Type material: 2 syntypes (MZUF 10820, 13121), one of which selected as lectotype (Figure 26).

Type locality: "Habitat prope Sassari."

Status: *Xerosecta dohmi* (Paulucci, 1882) see Manganelli et al. (1995).

Helix Hillyeriana Paulucci, 1882:251–252, 1883: pl. 7, fig. 4, 4a–d.

Type material: In Paulucci collection there are three lots of *Helix hillyeriana* (11503 + 13122, 11504, 11505). One contains a juvenile specimen (11505), another a specimen assigned to a "forma minor" (11504), and the last (11503 + 13122) three adult shells, one of which (11503) is figured by Paulucci (1883). This specimen (11503) is designated as the lectotype (Figure 25).

Type locality: "Habitat in locu Decimomannu dicto, insulae Sardiniae."

Status: *Xerosecta hillyeriana* (Paulucci, 1882) see Manganelli et al. (1995).

Helix parva Pfeiffer, 1848:441–442.

Type material: no syntypes are known. In the Forschungsinstitut und Naturmuseum Senckenberg (Frankfurt a.M., Germany) there is a lot of four specimens (SMF 10224), which could have been presented by L. Pfeiffer. One of these (Figure 27) is figured by Kobelt (1878: pl. 152, fig. 1548).

Type locality: "in Sardinien."

Status: a nominal species of *C. (Cernuella)* in need of revision.

Helix tuta Paulucci, 1882:245–248, 1883: pl. 7, figs. 1, 1a, b.

Type material: In Paulucci Collection there are many lots of *Helix tuta*: four from Selinunte (Sicily) (MZUF 11506, 11518, 11519, 11520), one from "anfiteatro di Cagliari" (MZUF 11517), the others from "i monti tra Sarroch e S. Pietro di Pula nella provincia di Cagliari" (MZUF 11507, 1508, 11509 + 13120, 11510, 11511, 11512, 11513, 11514, 11515, 11516). All of the latter, except 11509, are assigned to distinct forms eg., *minor zonata* (11507), *minor* (11508, 11517), *zonata* (11510), *minima* (11511), *elata* (11512), *elata zonata* (11513), *minima zonata* (11514), *minor pallescens* (11515), and *pallescens* (11516). One (11509) of the eight specimens of 11509 + 13120 corresponding to that figured by Paulucci (1883), is selected as the lectotype (Figure 24).

Type locality: "Abita sui monti tra Sarroch e S. Pietro di Pula nella provincia di Cagliari e l'anfiteatro della città omonima. La conosco pure di Sicilia ed i miei esemplari di questa provenienza mi vennero donati dal professor Hillyer Giglioli il quale li aveva raccolti presso Selinunte [It lives in the mountains between Sarroch and S. Pietro di Pula in the province of Cagliari and the amphitheatre of this town. I know it from Sicily; the Sicilian specimens were given to me by professor Hillyer Giglioli who collected them near Selinunte]." Following the designation of the lectotype the type locality is restricted to "monti tra Sarroch e S. Pietro di Pula nella provincia di Cagliari."

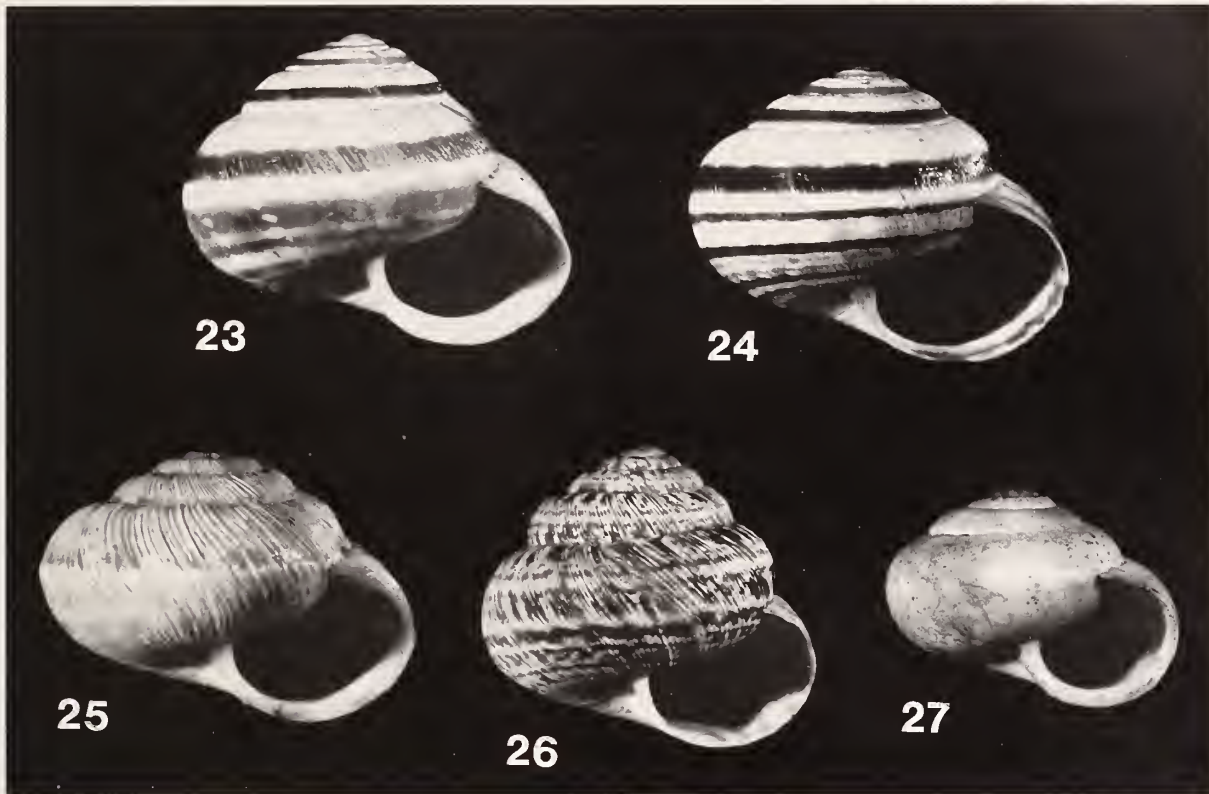
Status: a nominal species of *C. (Cernuella)* in need of revision.

the base of the penial papilla to the penis wall, a severely degenerated inner stylophore (except in *X. peloponnesia*) represented by a large cavity around the upper part of the basal portion and the vagina. Moreover, the species of *Xeromunda*, except *X. thessalica* Hausdorf, 1990, have only two tufts of digitiform glands on one side of the vagina. Other species, e.g., *X. peloponnesia* and *X. vulgarissima* (Mousson, 1859), also have a long flagellum (length of epiphallus plus penis) (for *Xeromunda* see Figure 28 [X. cf. *durieui* (Pfeiffer, 1848)], Figure 29 [X. *peloponnesia*], and Hausdorf, 1988: figs. 18, 19 [X. *candioti* (Pfeiffer, 1848)], Manganelli & Giusti, 1989: figs. 1A–F, 2A–L, 3E, 5B [X. cf. *durieui*], figs. 3A–D, 4A–F [X. *candioti*], Hausdorf, 1990: figs. 1–3 [X. *candioti*], figs. 4–6 [X. *peloponnesia*], figs. 7–10 [X. *vulgarissima*], figs. 12–14 [X. *thessalica*]; for *Xerolenta* see Hausdorf, 1988: 22, 23, fig. 17 [X. *obvia* (Menke, 1828)]).

Pseudoxerophila deserves special attention because, besides the basal portion, it shares a similar inner stylophore structure, i.e., long, slender, with thin walls and wide lumen, bent to adhere to the upper side of the basal portion, with *Ichnusomunda* (and *X. peloponnesia* the taxonomic status of which needs to be reconsidered). *Pseudoxerophila* and *Ichnusomunda* also share a very short proximal penis and a long left lateral lobe of the pallial margin. Again *Pseudoxerophila* differs from *Ichnusomunda* in having cerebral innervation of the penis and 2 + 2 dart-sac complex (for the only known species of *Pseudoxerophila*, *P. bathytera* (Westerlund & Blanc, 1879), see Figure 30 and Hausdorf, 1989:20–22, figs. 14–16).

Before concluding, a note about *Polloneriella* is warranted. This taxon has recently been proposed as a subgenus of *Xerosecta* (Manganelli & Giusti, 1988). The only species of *Polloneriella*, *P. contermina* (Pfeiffer, 1848), has genitalia that are quite characteristic with respect to those of the typical subgenus (re-examination of its rank and relationships is necessary), particularly by the fact that the two stylophores are inside a bilobe swelling of the vagina walls that somewhat imitates the basal portion of the dart-sac complex in *Ichnusomunda*. Nevertheless, they are quite unrelated: apart from the cerebral innervation of its penis, *Polloneriella* is easily distinguished by an inner stylophore slightly smaller than the outer and clearly evident, situated side-by-side with the outer (its longitudinal axis is parallel to that of the outer); the peculiar shape of the dart; a penial papilla without frenula, and with a different transverse section (for the only known species of *Polloneriella*, *P. contermina* (Pfeiffer, 1848) see Manganelli & Giusti, 1988:354, figs. 10A–E, 14G).

The remaining genera have no significant characters in common with *Ichnusomunda*, apart from the dart-sac complex and the right ommatophore free of the genitalia (*Helicopsis*, *Helicotricha*, *Xeropicta*, and *Xerotricha*), the 0 + 2 DSC (*Microxeromagna*), and the very short prox-



Explanation of Figures 23 to 27

Type and historical specimens of nominal taxa of the species group introduced for Sardinian xerophilous hygromiids. Lectotype of *Xerophila balteata* Pollonera, 1892 from "Tudu Mannu presso Cagliari," Pollonera collection, Museo Regionale di Scienze Naturale (Turin, Italy) MRSNT no. 149/A. Lectotype of *Helix tuta* Paulucci, 1882 from "Monti tra Sarroch e S. Pietro di Pula," Paulucci collection, Museo di Zoologia dell'Università di Firenze (Florence, Italy), MZUF no. 11509. Lectotype of *Helix hillyeriana* Paulucci, 1882 from "Decimomannu," Paulucci collection, Museo di Zoologia dell'Università di Firenze (Florence, Italy), MZUF no. 11503. Lectotype of *Helix dolrni* Paulucci, 1882 from "Sassari," Paulucci collection, Museo di Zoologia dell'Università di Firenze (Florence, Italy), MZUF no. 10820. Shell of *Helix parva* Pfeiffer, 1848, figured by Kobelt (1878: pl. 103, fig. 1548), Forschungsinstitut und Naturmuseum Senckenberg (Frankfurt A. M., Germany), SMF no. 10224. All $\times 4$.

imal penis (*Xerosecta*). Consequently, they will not be further discussed (for *Helicopsis* see Giusti & Manganelli, 1989 and Giusti et al., 1992; for *Helicotricha* see Giusti et al., 1992; for *Xeropicta* see Schileyko, 1978; for *Xerotricha* see Giusti & Manganelli, 1989; for *Microxeromagna* see Manganelli & Giusti, 1988; for *Xerosecta* see Manganelli & Giusti, 1988 and Manganelli & Favilli, 1996).

From the above discussion it is evident that *Ichnusomunda* shares anatomical character-states with two separate groups of helicelline hygromiids (i.e., *Cermuella* and its allies vs. *Xeromunda*, *Xerolenta*, and *Pseudoxerophila*). This may occur in three ways. *Ichnusomunda* may share a set of character-states with *Cermuella* through common ancestry and another set with *Xeromunda*, *Xerolenta*, and *Pseudoxerophila* through homoplasy; or it may share a set of character-states with *Xeromunda*, *Xerolenta*, and *Pseudoxerophila* through common ancestry,

and another set with *Cermuella* through homoplasy; or it may share both sets of character-states with *Cermuella* and *Pseudoxerophila*-*Xerolenta*-*Xeromunda* through common ancestry (i.e., as plesiomorphic states with respect to the larger group that contains all three groups of taxa) without any homoplasy. The only way to choose between these three possibilities is to have a phylogenetic hypothesis based on other characters. We regard these character-states (pedal innervation of penis, long left lateral lobe of pallial margin, frenula in penial papilla, basal portion of dart-sac complex, and inner stylophore of *Ichnusomunda*-type) as apomorphic which means that the anatomy of *Ichnusomunda* is subject to homoplasy. We derived this interpretation from the fact that all the possible sister groups of the larger group containing the three groups of taxa (whatever they are: hygromiids or even another, larger helicoid group) never have these character-states, which only appear in the hygromiid genera cited.

Table 2

List of the main characters used in the discussion of the relationships of *Ichnusomunda*.**1—Penial nerve**

- Penial nerve from right cerebral ganglion = A
 Penial nerve from right pedal ganglion = B

2—Left lateral lobe

- Left lateral lobe short (the distance between the upper vertex of LLL and the lower of LDL is equal to or greater than the length of LLL) = A
 Left lateral lobe medium- to long (the distance between the upper vertex of LLL and the lower of LDL is very short) = B

3—Dart-sac complex (number of stylophores forming the DSC on opposite side of vagina)

- Dart-sac complex 0 + 2 = A
 Dart-sac complex 2 + 2 = B

4—Vagina and dart-sac complex

- Dart-sac complex symmetrically disposed with respect to vagina (it is possible to divide the dart-sac complex and vagina longitudinally into two specular halves) = A
 Dart-sac complex asymmetrically disposed with respect to vagina (it is not possible to divide the dart-sac complex and vagina longitudinally into two specular halves) = B

5—Basal portion of dart-sac complex

- Dart-sac complex without basal portion = A
 Dart-sac complex with out basal portion, but with two stylophores sunk between two large vaginal swellings = B
 Dart-sac complex with cylindrical, more or less developed basal portion joined perpendicularly to distal vagina = C

6—Shape and size of inner stylophore

- Inner stylophore saclike but very elongated (Schileyko, 1978: fig. 245) = A
 Inner stylophore saclike, approximately same size as, or slightly smaller than, outer stylophore (Giusti & Manganelli, 1989: fig. 9D) = B
 Inner stylophore of *Xerotricha*-type (inner stylophore saclike, markedly smaller than outer stylophore and with only its apical part visible from outside; Giusti & Manganelli, 1989: fig. 9A) = C
 Inner stylophore of *Helicella*-type (inner stylophore vestigial, not visible from outside, reduced to form a small cavity between vagina and large, bottle-shaped outer stylophore; Giusti & Manganelli, 1989: fig. 9C) = D
 Inner stylophore of *Ichnusomunda*-type (saclike approximately same size as, or larger than, outer stylophore, more or less elongated with thin walls and large lumen and, bent to adhere to upper side of basal portion, this paper: Figure 27) = E
 Inner stylophore of *Xeromunda*-type (severely degenerated, represented by a large cavity around the upper part of the basal portion and the vagina; this paper: Figure 28) = F

7—Dart-sac complex opening into vagina

- Stylophore openings between two pleats not larger than other vaginal pleats = A
 Stylophore openings between two large U-shaped vaginal pleats = B

Stylophore openings in the basal portion of dart-sac complex, between two large U-shaped pleats originating in proximal vagina = C

Stylophore openings in large tonguelike structure (two distinct tonguelike structures in the case of 2 + 2 DSC; Giusti & Manganelli, 1989: fig. 9A) = D

Stylophore openings in large tonguelike structure which forms a single tubelike structure in the case of 2 + 2 DSC and sometimes in the case of 0 + 2 DSC derived from 2 + 2 DSC ? (Giusti & Manganelli, 1989: figs. 9C) = E

Stylophore openings in groove of structure similar to a dart-gun, but simpler and shorter than that of other hygromiids, open as far as tip = F

Stylophore openings in groove of dart-gun, having short, closed tip = G

Stylophore openings in dart-gun, having large, closed, cylindrical muff and small tip = H

8—Dart

Cernuella-type (straight or slightly curved with rounded or polygonal section for most of length; transverse section of tip rhombic or in form of cross with two opposite arms longer than other two) = A

Microxeromagna-type (straight or slightly curved with two opposite lateral wings for most of its length and rhombic section) = B

Polloneriella-type (straight or slightly curved with one lateral wing for most of its length and rhombic section) = C

Xeroplana-type (straight or slightly curved with rhombic section and hook-like projection) = D

9—Flagellum

Flagellum short- to medium (approximately one-fourth length of the epiphallus plus penis) = A

Flagellum very long (approximately equal to length of epiphallus plus penis) = B

10—Frenula connecting penial papilla base with penial walls

No frenula = A

Three frenula = B

11—Transverse section of apical penial papilla

Cernuella-type (wall of penial papilla solid, with some small lacunae) = A

Helicopsis-type (wall of penial papilla with three lacunae all around central lumen, at least in *H. striata*) = B

Helicotricha-type (wall of penial papilla solid, with T-shaped pilaster alongside its entire length, joined to penial papilla by a peduncle) = C

Polloneriella-type (wall of penial papilla separated into peripheral and central portions by large annular lacuna) = D

Microxeromagna-type (wall of penial papilla very thin and open along one side) = E

Xerosecta-type (wall of penial papilla with pilasters and lacunae to imitate corpora cavernosa) = F

12—Appendix in the distal genitalia

absent = A

penial = B

Table 3

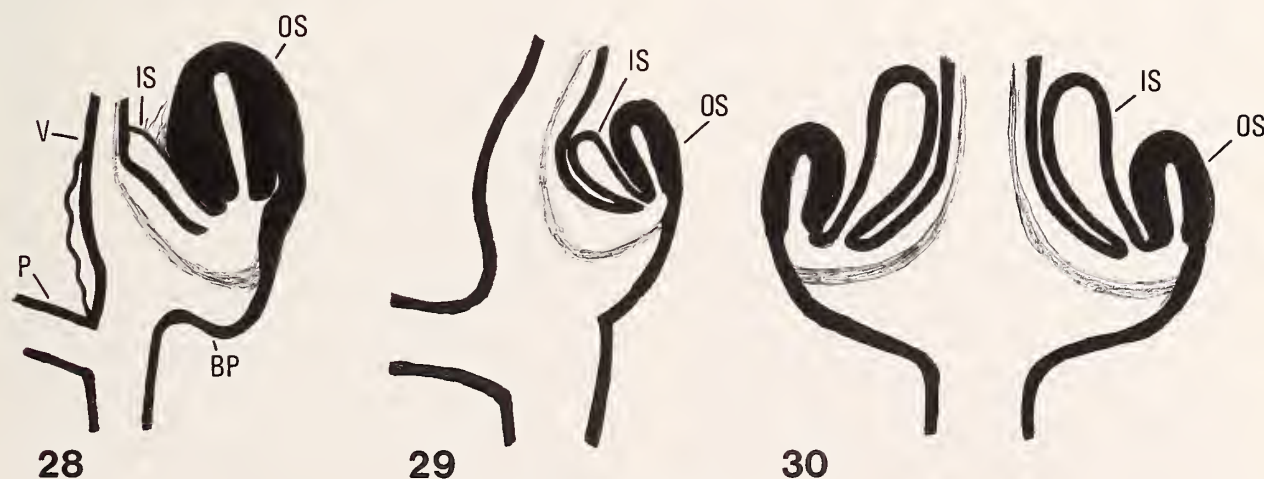
List of taxa and main characters cited in the discussion. All the taxa listed have a right ommatophore free of the genitalia and a dart-sac complex (consisting of an inner dartless stylophore and an outer dart-secreting stylophore).

	1	2	3	4	5	6	7	8	9	10	11	12
<i>Candidula</i>	B	A	A	A	A	D	E	A	AB	A	A	A
<i>C. (Cernuella)</i>	B	B	A	A	A	B	G	A	A	B	A	A
<i>C. (Xeroamanda)</i>	B	B	A	A	A	B	G	A	A	B	A	A
<i>C. (Xerocincta)</i>	B	B	A	A	A	B	G	A	A	A	A	A
<i>Cernuellopsis</i>	B	A	A	B	A	B	H	A	A	A	A	A
<i>Helicella</i>	B	A	B	A	A	D	E	A	A	A	A	A
<i>Helicopsis</i>	A	A	B	A	A	B	AB	A	A	A	B	A
<i>Helicotricha</i>	A	A	B	A	A	B	B	A	B	A	C	A
<i>Ichnusomunda</i>	B	B	A	A	C	E	C	A	A	B	A	A
<i>Microxeromagna</i>	A	A	A	A	A	A	A	B	B	A	D	A
<i>Polloneriella</i>	A	A	A	A	B	B	A	C	A	A	E	A
<i>Pseudoxerophila</i>	A	A	B	A	C	E	B	A	B	A	A	A
<i>Xerolenta</i>	A	A	B	A	C	F	C	A	A	A	A	A
<i>Xeromunda</i>	A	A	A	A	C	F	C	A	AB	A	A	A
" <i>Xeromunda</i> " <i>peloponnesia</i>	A	A	A	A	C	E	?	A	B	A	A	A
<i>Xeroplana</i>	B	B	A	A	A	B	F	D	B	A	A	A
<i>Xeropicta</i>	?	?	B	A	A	A	?	?	A	A	?	B
<i>Xerosecta</i>	A	A	A	A	A	B	A	A	A	A	F	A
<i>Xerotricha</i>	A	A	B	A	A	C	D	A	A	A	AB	A

If the pedal penial innervation is a good character to identify monophyly of the group which includes *Candidula*, *Cernuellopsis*, *Cernuella* (*Cernuella*), *Cernuella* (*Xeroamanda*), *Cernuella* (*Xerocincta*), *Helicella*, and *Xeroplana*, then *Cernuella* (*Cernuella*) and *Cernuella* (*Xeroamanda*) are the closest to *Ichnusomunda*. This conclusion is supported by the fact they share at least one synapomorphy: three frenula at the base of the penial papilla. If so, a profound, autoapomorphic modification of

the dart-sac complex distinguishes *Ichnusomunda* from *Cernuella*. This modification produced an organization of the dart-sac complex which is homoplastic for two characters (basal portion of dart-sac complex; inner stylophore of *Ichnusomunda*-type) with respect to that in another group of taxa of the helicellids, the group including *Xeromunda*, *Xerolenta*, and *Pseudoxerophila*.

The alternative interpretation, the basal portion of dart-sac complex, identifying the putative monophyletic group



Explanation of Figures 28 to 30

Scheme of dart-sac complex of *Xeromunda candiota* (Pfeiffer, 1848), *X. peloponnesia* Hausdorf, 1990, and *Pseudoxerophila bathytera* (Westerlund & Blanc, 1879). Key: BP, basal portion of dart-sac complex; GA, genital atrium; IS, inner stylophore; OS, outer stylophore; P, penis; V, vagina.

Ichnusomunda-*Xeromunda*-*Xerolenta*-*Pseudoxerophila*, in which *Pseudoxerophila*, *Ichnusomunda*, and *X. peloponnesia* are more primitive due to the less derived structure of the inner stylophore) obviously implies that the pedal penial innervation, the long left lateral lobe of pallial margin and the penial papilla with three basal frenula of *Ichnusomunda* are of a homoplastic nature.

Anatomical research for future cladistic analysis is currently underway on the different taxa of the genus group of the hygromiids. Until the results of this research are available, the first interpretation seems more probable on the basis of the characters involved (pedal innervation of penis, long left lateral lobe of pallial border, and penial papilla with three frenula) and biogeographical data (*Xeromunda*, *Xerolenta*, and *Pseudoxerophila* have a prevalent E-Mediterranean distribution; *Cernuella* and the new species are prevalently W-Mediterranean).

Irrespective of this tentative conclusion, the genital structure of *Ichnusomunda* shows a clear case of homoplasy. The case, certainly not unique in the hygromiids or in the helicoids in general, suggests prudence in the common practice of inferring phylogeny and splitting taxa above the genus level on the basis of genital characters.

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